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THE MORPHOLOGICAL RELATIONSHIPS OF THE FLORIDEAE AND THE ASCOMYCETES

By B. O. DODGE

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The morphological relationships of the Florideae and the Ascomycetes

B. O. Dodge

(with thirteen text figures)

In recent years our knowledge of the structure and life processes of many species of algae and fungi has been increased by general morphological studies frequently supplemented by critical cytological investigations. The later literature contains a vast amount of data bearing more or less directly on the question of the phylogenetic relationship of the Florideae and Ascomycetes. Harper has clearly distinguished between the questions of morphological relationship and those relating to the special functional activities of the initial organs of the ascocarp.

In the present paper I shall still further discuss the morphology of the various reproductive structures of the Florideae and Ascomycetes in the light of my recent observations on the trichogynes and ascogonia in various members of the Ascobolaceae and related forms (37). Practically all the recently accumulated evidence favors the view that the Ascomycetes are a monophyletic group and have been derived from the red algae. I have brought together in the form of diagrams the results of both recent and older work bearing on this question. The transition from the conditions in the red algae to those in the Collemaceae as described by Stahl (86) has been made much clearer by the work of Miss Bachmann (2, 3) in her studies on *Collema pulposum*.

Brefeld's doctrine that the Ascomycetes have been derived from the Phycomycetes through the evolution of the sporangium into the ascus is of course untenable, though in a somewhat modified form it has been recently revived by Bucholtz (21), who regards *Endogone* as a true Phycomycete in which the fruit resulting from the fusion of the nuclei from two unequally differentiated sex cells is a "zygosporocarp." The short time in which the sex nuclei travel together as a pair out of the oögonium directly into the sac-like outgrowth of the oögonium where they fuse, suggests to Bucholtz a primitive binucleated condition such as might have

existed just previous to the inauguration of the habit of conjugate nuclear division which leads to the fusion of the nuclei in the ascus of such Ascomycetes as *Galactinia*, *Acetabula*, and *Pyronema* according to Claussen (26).

The question as to the relationship of the outgrowths of the fertilized egg, ascogenous hyphae, in the Ascomycetes and oöblastema filaments in the red algae is fundamental for the understanding of the phylogeny of the two groups, and it is a question that has been much neglected. It is a conspicuous and well-established fact that it is an essential character of the eggs in both groups to give rise to more or less complex filamentous outgrowths immediately after fertilization. De Bary (5), although he suspected from what he knew of the mildews that the ascus must in all cases be an outgrowth of the fertilized egg, was unable to trace the connection in *Pyronema*. Kihlman (57) succeeded in making out this connection and it was thus established that the asci are regularly the end members of outgrowths of the oögonium, although Brefeld, in spite of the fact that all subsequent investigations based upon the careful use of microtome sections proved the contrary, continued to insist that the asci might arise from the same hyphae as the paraphyses. Curiously enough Blackman and Welsford (12) notwithstanding the abundant evidence to the contrary in other cases, and the fact that they find a well-developed ascogonium at the origin of the ascocarp, arrive at the conclusion that in *Polystigma* the asci do actually arise from the vegetative hyphae. Fisch (41) recognized the difference between the purely vegetative clusters of hyphae which penetrate the stomata and the trichogynes which are found surrounded by these "respiratory hyphae" (FIG. 1, D). The trichogyne could be distinguished on account of its size and the characteristic changes occurring in it on the application of reagents. Blackman and Welsford (12) have recently reinvestigated this species and are unable to discover that the ascogonium ever develops a trichogyne which grows outward through a stoma, although they figure a trichogyne-like hypha directed outward toward a stoma. They suspect that the trichogyne described by Fisch was merely one of the vegetative hyphae crowding through the stoma just as they do in *Gnomonia*, where Brooks (17) calls them trichogynes that are now sexually function-

less and have probably taken on a respiratory function. It is difficult to understand how Fisch could have figured such perfect ascogonia and trichogynes without having before him the actual structures in question. That he did see ascogonia is attested by the very similar structures figured by Blackman and Welsford and it is not altogether clear how an ascogonium which lies at the very center of the developing perithecium could be uncoiled and forced practically to the wall as they describe unless it were concerned in the production of the ascogenous hyphae which as a fact come to occupy much of the central space of the perithecium.

The first convincing proof that the asci develop from the hyphae arising from the ascogonium was furnished by Janczewski (56) for *Ascobolus furfuraceus* (FIG. 9, B), and shortly afterwards Borzi (15) found practically identical conditions prevailing in *Ascophanus pilosus* (*Lasiobolus equinus*). Undoubted connections between ascogonia and asci have been traced in a number of species. Among the forms in which this connection has been quite satisfactorily established we may note the following: *Sphaerotheca Castagnei* (De Bary, 1863), *Ascobolus furfuraceus* (Janczewski, 1871), *Lasiobolus equinus* (Borzi, 1878), *Pyronema confluens* (Kihlman, 1883), *Sphaerotheca Castagnei* (Harper, 1895), *Ascobolus furfuraceus* (Harper, 1896), Laboulbenieae (Thaxter, 1896), *Pyronema confluens* (Harper, 1900), *Poronia punctata* (Dawson, 1900), *Pertusaria communis* (Baur, 1901), *Gymnoascus candida* (Dale, 1903), *Phyllactinia corylea* (Harper, 1905), *Ascodesmis nigricans* (Claussen, 1905), *Humaria granulata* (Blackman & Fraser, 1906), *Thelebolus stercorarius* (Ramlow, 1906), *Thecotheus Pelletieri* (Overton, 1906), *Lachnea stercorea* (Fraser, 1907), *Aspergillus herbariorum* (Fraser & Chambers, 1907), *Baeomyces roseus* (Nienberg, 1907), *Usnea barbata* (Nienberg, 1907), *Ichmadophila aeruginosa* (Nienberg, 1907), *Aspergillus repens* (Dale, 1909), *Ascophanus carneus* (Cutting, 1909), *Gnomonia erythrostoma* (Brooks, 1910), *Leotia chlorocephala* (Brown, W. H., 1910), *Lachnea scutellata* (Brown, W. H., 1911), *Pyronema confluens* (Claussen, 1912), *Ascobolus carbonarius* (Dodge, 1912), *Laboulbenia chaetophora* (Faull, 1912), *Collema pulposum* (Bachmann, 1913), *Xylaria tentaculata* (Brown, H. B., 1913), *Lachnea cretea* (Fraser, 1913).

It is certainly one of the best established facts in the mor-

phology of the Ascomycetes that the asci arise from outgrowths of the ascogonia and that the paraphyses do not originate in the same manner or from the same cells. A further interesting feature in this connection is found in the fact that, in certain forms like *Pyronema*, the mildews, *Ascobolus furfuraceus*, *Lasiobolus equinus*, etc., only one cell gives rise to ascogenous hyphae, while in *Thecotheus* (70), *Ascophanus carneus* (27), *Ascobolus glaber* (31), *A. carbonarius* (37), *Lachnea cretea* (44), and in the lichens (FIG. 7), so far as this process has been noted (9, 32, 65, 3), there are several ascogenous cells in the ascogonium.

As noted above, De Bary (5) discovered that the apothecium of *Pyronema* originates from a rosette of paired swollen hyphae, and his figures show correctly the general form of these hyphae and the tube-like structures connecting the pairs. Bornet and Thuret published their account of fecundation in the red algae in 1867 (14) and gave the name trichogyne to the receptive elongation of the carpogonium. The following year we have the first clear statement of the morphological resemblance between the reproductive structures of the red algae and the Ascomycetes as represented by *Pyronema*. Sachs (75) noted the likeness of the oögonium with its trichogyne to the corresponding structures in the Florideae and likewise the similarity of the fruit body of the Ascomycetes to that of such forms as *Lejolisia* (FIG. 6, F). He also pointed out the difference between the antheridia of *Pyronema* and those of the red algae. Judging from Sachs' repeated references to De Bary in this connection it is not at all unlikely that it was De Bary who originally pointed out these similarities, for in 1870 (4) he states very clearly the evidence upon which a relationship between the two groups might be assumed. He showed also how it might be possible to derive the Ascomycetes from such forms as *Peronospora*, but at this time he maintained that the evidence at hand was not sufficient to justify a conclusion in favor of either hypothesis. His latest attitude on this question may perhaps be inferred from a note by Sachs (76) where it is said in reference to the derivation of the Ascomycetes from the Rhodophyceae: "von den Rhodophyceen sind die Ascomyceten (oder wenigstens die Discomyceten) abzuleiten, worauf vorwiegend die Procarpien beider hinweisen"; to which is added the footnote, "soweit ich

privatim unterrichtet bin, war sowohl De Bary wie Schmitz dieser Annahme zugeneigt."

Woronin, Janczewski, De Bary, and Borzi do not specifically identify the tapering end of the ascogonium in *Ascobolus* as a trichogyne though they give no other interpretation of this very important structural feature of the egg apparatus, and Sachs' classic figure of *A. furfuraceus* represents the fertilization as occurring by means of a pollinodium which applies itself to the tip of the many-celled ascogonium, though this conception has by no means been held by all subsequent students of the form. Stahl's work on the lichens established beyond question the existence of trichogynes fertilized by free spermatia, and this is probably the most important discovery bearing on the relationship of the two groups.

Among the Ascomycetes the trichogyne is most characteristically developed in the Laboulbenieae. The variability in the form of the trichogynes in this group is almost without limit. They may be one-celled structures as in *Stigmatomyces Baeri* (FIG. 2, G), recalling the trichogyne of *Batrachospermum* (FIG. 4, B), or they may be multicellular spirally coiled and branched as in *Compsomyces verticillatus* (FIG. 2, I). Some of them are very similar to the trichogyne of *Pyronema* (FIG. 2, D), as in *Zodiomyces vorticellarius* (FIG. 2, J), where the spermatia remain attached to the stalk, and the trichogyne is therefore a structure active in seeking out the spermatia.

Ascodesmis, a form closely related to *Pyronema*, furnishes a further example of a reduced trichogyne. Claussen (25) finds that the end cell of the short spiral coil of the ascogonium functions as a trichogyne (FIG. 2, E). It is not especially different in structure from the other cells of the ascogonium.

Kihlman (57) did not consider the tapering end of the ascogonium of *Melanospora* as a trichogyne (FIG. 2, K) for the reason that he was unable to find that it fused with any hypha representing an antheridium. Miss Nichols (64), however, reports in *Hypocopra* and *Ceratostoma* (FIG. 2, C), other members of the same group, that the end cell of the ascogonium does connect with an antheridium.

Fraser and Chambers (46) find that the ascogonium of *Asper-*

gillus herbariorum is provided with an end cell that functions as a trichogyne in certain cases. They think this form is becoming apogamous, but this fact would not, in their opinion, affect the question of the homologies of the cells at the end of the archicarp.

I have described a form of archicarp in *Ascobolus carbonarius* which in its origin is entirely unlike any hitherto known in the Ascomycetes. I refer to the common form of the species which produces abundant spore-like bodies, "conidia," on long stalks, and not to the form *A. mirabilis* (37) of Dangeard. This latter strain which I have since isolated and grown several months in pure cultures produces the ascogonium directly from the mycelial hyphae only rarely producing conidia, and then only in very old cultures. Other interesting abnormalities in the archicarp crop out frequently in this strain. I have not been able to follow the development of these abnormal forms but they do not seem to give rise to normal apothecia.

The typical ascogonia of *A. carbonarius* develop apothecia in about two weeks. As described (37), most frequently the ascogonium arises directly from what appears to be an asexual conidium which germinates forming a coiled portion. The original germ tube thus becomes the stalk of the archicarp at the end of which is formed a second coil of extremely large cells composing the ascogonium proper, and from this is derived by sudden constriction of the end cell a long irregularly coiled trichogyne (FIG. 1, E) which in general is not very unlike the trichogyne of *Collema pulposum* (FIG. 1, C) described by Miss Bachmann (2, 3). When grown in artificial media the trichogyne winds about in the medium or on its surface somewhat irregularly and in many cases the long end cell comes in contact with other conidia on long stalks, which I have called antheridial conidia (FIGS. 1, E, and 3, B). The trichogyne end coils itself tightly about this antheridial conidium in such a manner as to indicate that there is a definite attraction between them. The resemblance of the antheridial conidia here to the spermatia of Miss Bachmann's *Collema* (FIGS. 1, C, and 3, D) is direct and striking. I do not know that any of these conidia of *A. carbonarius* function as asexual bodies in distributing the species. They do not become detached from their stalks and are not oriented as we should expect functional conidia

to be. The conidia of *Lachnea abundans* are very loosely attached to erect aerial conidiophores and germination takes place as soon as they are brought into a fresh medium. In my cultures these conidia of *A. carbonarius* never function in any other way than that described. They never produce mycelia directly. Aborting ascogonia do sometimes grow out vegetatively into long hyphae but such growths are recognizable at once and would not be mistaken for trichogynes. The trichogyne is a hypha of very uniform diameter terminating rather bluntly and without branches (FIG. 1, E).

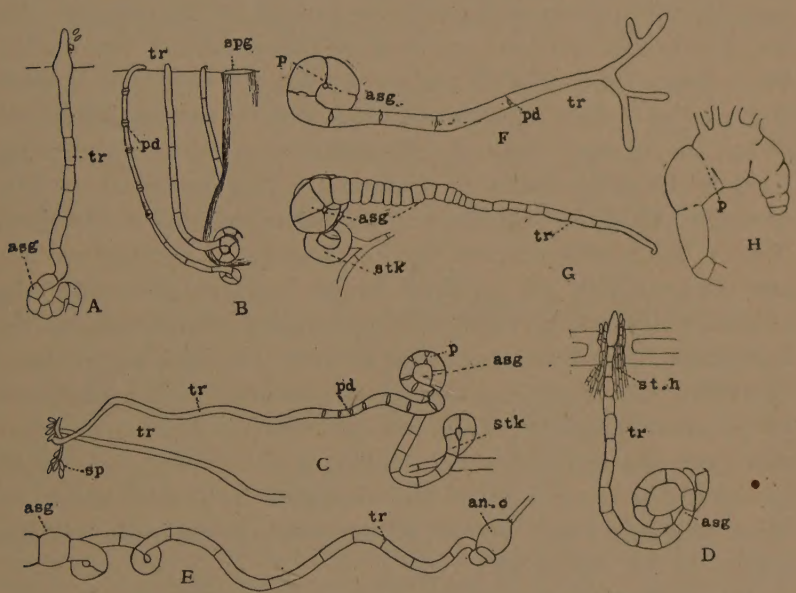

FIG. 1. Septate trichogynes of Ascomycetes. A. *Collema microphyllum;* B. *Physma compactum;* C. *Collema pulposum;* D. *Polystigma rubrum;* E. *Ascobolus carbonarius;* F. *Lachnea cretea;* G. *Lachnea melaloma;* H. *Ascobolus furfuraceus. asg,* ascogonium; *an.c,* antheridial conidium; *p,* pore in cross wall; *pd,* callous pad; *spg,* spermogonium; *st.h,* sterile hyphae; *stk,* stalk of ascogonium; *tr,* trichogyne. A, B, Stahl; C, Bachmann; D, Fisch; F, Fraser; H, Harper; E, G, original.

The importance of Miss Bachmann's work on *Collema pulposum* can scarcely be overestimated since it furnishes perhaps the most convincing evidence in support of the view that the spermatia of the lichens are sexual organs and that their trichogynes are morphologically equivalent to those of the red algae and of *Pyro-*

nema. Miss Bachmann finds that the spermatia of *C. pulposum* are not borne in spermogonia as they are in the forms described by Stahl and others, but are borne singly or in small numbers on branches from the vegetative hyphae imbedded deeply in the thallus (FIGS. 1, C, and 3, D). These spermatia never find their way to the surface of the thallus and commonly remain loosely attached to the spermatiophores. The general character of the fertile branch is not unlike that of other Collemas (FIG. 1, A and B) except as to the structure of the trichogyne and its behavior in fertilization. The specific attraction which the spermatia have for the trichogyne is positively proved by the fact that the trichogyne does not bore outward to the surface of the thallus but is compelled to wind in and out among the vegetative hyphae and colonies of algae in order to connect with the spermatia isolated within the thallus. Several trichogynes may be found growing towards the same cluster of spermatia. The somewhat swollen receptive cell of the trichogyne of the lichens heretofore described (FIG. 1, A) is well adapted for its purpose. Extensive surface area and stability are provided by its increased diameter. In *Collema pulposum*, by virtue of the certainty with which the tip is directed toward the spermatia, no such provision is necessary. However, the receptive surface here is probably much increased by the great elongation of the end cell, which in some cases occupies over one half the entire length of the trichogyne. Wolff (94) describes the end cell of the trichogyne in *Graphis elegans* as being extremely long. In fact no septa were found in the vertical portion of the trichogyne.

The trichogyne of *Lachnea stercorea* (FIG. 2, B) described by Miss Fraser (45) represents another type intermediate between those of *Pyronema* and *Collema*. It is a thick five- or six-celled outgrowth of the oögonium and curves downward fusing with a long irregular club-shaped cell which Miss Fraser believes is an antheridium.

The trichogynes in the lichens, *Ascobolus carbonarius*, and *Lachnea stercorea* are quite as strongly developed as the corresponding organs in the red algae. The land habit has, however, led to their reduction and even disappearance in many forms of Ascomycetes.

The ascogonium of *Lachnea scutellata* (Woronin, 96, W. H. Brown, 19) is not known to have a trichogyne. These authors examined only the comparatively well-developed young fruits and were of course unable to determine the exact form of the archicarp.

Miss Fraser's latest paper (44) describes the trichogynes of *Lachnea cretea* (FIG. 1, F) as long and branching. No antheridium was found and Miss Fraser regards the form as wholly apogamous. The archicarps of *L. cretea* as described are very similar to those of *L. abundans*, which I have been able to grow and bring to maturity in great numbers in artificial cultures. In *L. cretea* the cross walls are sometimes perforated but later these perforations

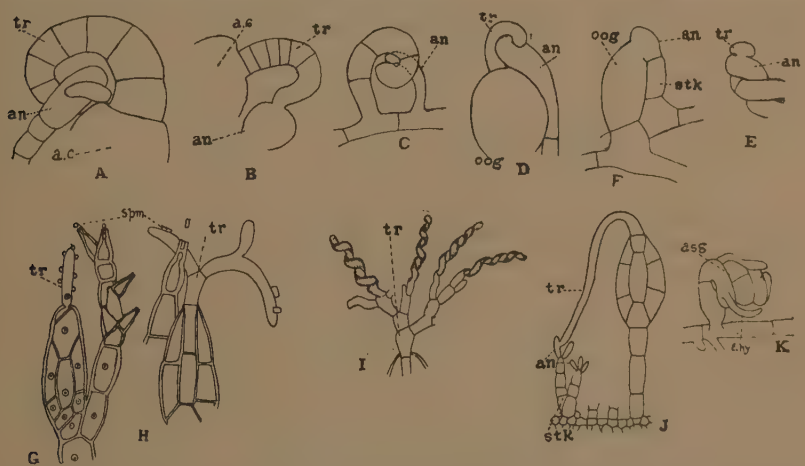

FIG. 2. The upper row shows a further reduction of the trichogyne and a correspondingly nearer approach of the antheridium to the oögonium. A. *Ascobolus magnificus;* B. *Lachnea stercorea;* C. *Ceratostoma;* D. *Pyronema;* E. *Ascodesmis;* F. *Sphaerotheca;* G–J. Four types of trichogynes found in the Laboulbeniaceae. G. *Stigmatomyces Baeri;* H. *Laboulbenia cristata;* I. *Compsomyces verticillatus;* J. *Zodiomyces vorticellarius;* K. The ascogonium of *Melanospora parasitica* without a trichogyne. *a.c*, ascogenous cell; *an*, antheridium; *asg*, ascogonium; *e.hy*, enveloping hyphae; *spm*, spermatium; *stk*, stalk; *oog*, oögonium; *tr*, trichogyne. A, original; B, Fraser; C, Nichols; D, F, Harper; E, Claussen; G, H, I, J, Thaxter; K, Kihlman.

are closed by thick pads. Miss Fraser believes that the antheridium has only recently disappeared. Branching trichogynes are not, however, confined to the Laboulbeniaceae as stated by this author. Stahl (86) figures a branched trichogyne in *Collema microphyllum*, Lindau (59) describes and figures such a form in

Lecanora subfusca, and Harper (53) figures a two-branched trichogyne in *Pyronema*. Miss Bachmann (3) also describes and figures a branch which is given off from the ascogonium at least very close to the base of the trichogyne in *Collema pulposum*.

The Tulasnes (90) mention the existence of an ascogonium in *Lachnea melaloma*. I have grown this form abundantly in cultures on agar media and find an archicarp of striking proportions. The long stalk, the many-celled coiled ascogonium prolonged into a trichogyne-like portion (FIG. 1, G), likewise the great irregularity and variety of forms which it shows in this species suggest a relationship with *Ascobolus carbonarius*. It may be even more

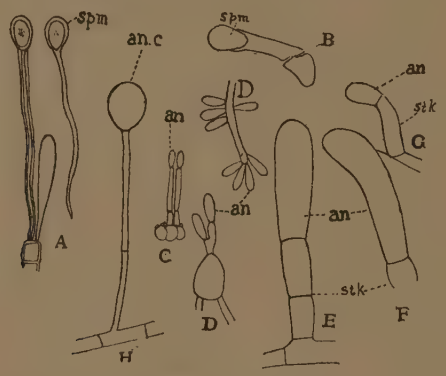

FIG. 3. Antheridia and spermatia. A. *Corallina officinalis;* B. *Delesseria sanguinea;* C. *Collema microphyllum;* D. *Collema pulposum;* E. *Ascobolus magnificus;* F. *Pyronema;* G. *Sphaerotheca;* H. *Ascobolus carbonarius*. *an*, antheridium; *an.c*, antheridial conidium; *spm*, spermatium; *stk*, stalk. A, Guignard; B, Svedelius; C, Stahl; D, Bachmann; F, Tulasne; G, De Bary; E, H, original.

closely related to the strain *A. mirabilis* since it produces no conidia, chlamydospores, or any asexual spore bodies whatever. The Tulasnes (90) figured conidia for *Pyronema;* later (89) they referred them to *Lachnea melaloma*. They undoubtedly were mistaken in both cases, as I find no such spores in my cultures. The archicarp of *Lachnea melaloma* frequently branches either in the region representing the trichogyne, or well back near the basal portion. In the latter case the branching is somewhat dichotomous. There is also a marked tendency to dichotomous branching in the vegetative hyphae.

As compared with the trichogynes of the Ascomycetes in

general the trichogyne of the red algae is a rather simple structure of quite constant type, being nothing more than an outgrowth or prolongation of the egg cell into a narrow tube. In certain cases, as in *Batrachospermum* (FIG. 4, B), it is a short club-shaped body projecting but little from the carpogonium. In *Nemalion*, *Liagora*, *Helminthora*, belonging to the Helminthocladiaceae, and perhaps in a majority of the species, it is a much longer thin filament (FIG. 4, F), which may be curved slightly to one side (FIG. 4, A). Somewhat more complicated are the trichogynes of *Dudresnaya*, *Polyides*, *Bonnemaisonia*, etc., where it is an extremely long and thread-like organ, several times spirally coiled near its base (FIG. 5, C). Some question exists as to whether or not the trichogyne possesses a nucleus of its own and is therefore an independent cell unit. It is commonly held that the trichogyne is simply an outgrowth of the egg cell, and that it is morphologically equivalent to the receptive spot in the egg of *Oedogonium*, *Vaucheria*, etc. Davis (34) claims that the trichogyne of *Batrachospermum* is provided with a chromatophore and nucleus of its own although there is no septum cutting them off from the egg. This has been denied by Osterhout (69) and Schmidle (77), and by Lewis (58) for *Griffithsia Bornetiana* also. Yamanouchi (97) is very positive in in his assertion that the trichogyne of *Polysiphonia* has a distinct nucleus.

No cases have been reported where a septum is found between the carpogonium and its trichogyne before fertilization. After fertilization it is commonly found that the egg is cut off from the trichogyne by a thickening of the narrow connecting portion, and Sturch (87) asserts that in *Harveyella mirabilis* a septum is laid down after fertilization between the trichogyne and carpogonium (FIG. 4, E). Harper has described the replacement of the wall, broken down during fertilization, for *Pyronema* (53). A similar method of blocking off trichogyne cells after fertilization has been described by Stahl, Baur, and Miss Bachmann for the lichens, and by Miss Fraser for *Lachnea cretea*. In many forms of the algae the carpogenic branch originates beneath the surface of the thallus. In such cases the trichogyne growing out obliquely from the carpogonium turns directly outward and penetrates any convenient opening between the surrounding filaments (FIG. 4, A). The object to

be gained is primarily to reach the surface, just as it is in the species of lichens described by Stahl (FIG. 1, A and B).

The most obvious difference between the Ascomycetes and red algae is found in the absence in the latter of anything like free cell formation. The ascus is the most characteristic and unique structure of the Ascomycetes. As De Bary and most of the earlier students of the group recognized, the process of free cell formation as found in the ascus is typically different from any

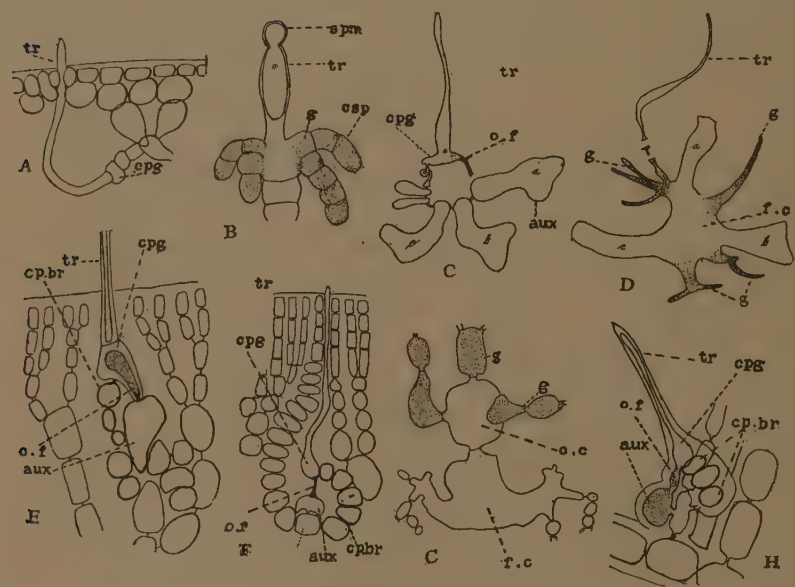

FIG. 4. Procarpic branch and outgrowths from the carpogonium in the red algae. A. *Halymenia ligulata;* B. *Batrachospermum moniliforme;* C, D, *Erythrophyllum delesserioides;* E. *Harveyella mirabilis;* F, G. *Prionitis Lyallii;* H. *Antithamnion Plumula. aux,* auxiliary cell; *c.c,* central cell; *cp.br,* carpogenic branch; *cpg,* carpogonium; *csp,* carpospore; *f.c,* fusion cell; *g,* gonimoblast; *o.f,* oöblastema filament; *spm,* spermatium; *tr,* trichogyne. A, Bornet; B, Davis; C, D, Twiss; E, Sturch; F, G, Daines; H, Phillips.

other method of spore formation known in the fungi. And the morphological characters of the ascus constitute the main difficulty in all attempts to derive the Ascomycetes from the Florideae. Recent cytological studies (Harper, 51) have emphasized the differences between free cell formation and the progressive cleavage found in sporangia, and Dangeard's discovery of nuclear fusion in

the young ascus (31) has seemed to indicate its resemblance to teleutospores and basidia rather than to any structures in the red algae. Dangeard first described the formation of the ascus in *Pustularia vesiculosa* as involving the fusion of two separate hyphae at their tips, a condition that was found later to actually be the method of origin of the binucleated basal cell in the aecidium cup of the rusts. Although Dangeard immediately corrected his error one can not doubt that it has been largely responsible for his whole theory of the sexuality and origin of the Ascomycetes. His views in this connection have received much attention and need not be considered further here, but the morphological features of the process by which an ascus is formed from the penultimate cell of a "hook" or "crosier" are so characteristic and of such widespread occurrence among the Ascomycetes as to warrant more careful examination than has been given to them. This sort of structure occurs in genera as widely separated as *Collema*, *Usnea*, *Lachnea*, *Morchella*, *Tuber*, *Aspergillus*, and *Pyronema*. In all some thirty-five species have been figured as showing the ascus formed in this manner, and nearly all conform to the same type. Harper (53), who first figured conjugate nuclear division in the hook, and others have given a great deal of attention to this phenomenon and have fully discussed the necessity for some such arrangement as a means of providing that the nuclei which fuse in the ascus shall not be sister nuclei. The manner in which the crosier may become modified seems to be almost without limit, but the fundamental principle is maintained with a very few exceptions. Faull (40) claims to have examined over thirty species and finds that the ascus arises from the penultimate cell invariably in eleven of them. In other forms he describes the omission of the wall which ordinarily cuts off the end cell so that in such cases the terminal cell gives rise to the ascus, although the hook is well represented with its tip curved down. Modifications of the hook by proliferation, the growing out of the end cell to form a second hook, or the fusion of the terminal cell with the antipenultimate cell are variations which have also been described. W. H. Brown (19, 20), McCubbin (61), Claussen (26), Fraser (43), and others have described further ways in which the crosier may be modified.

So far the crosier has not been homologized with any structure in the life history of the red algae. It seems to me that the possible relations of its characteristic features and the resulting fusion of non-sister nuclei to the secondary fertilizations of Schmitz deserve careful consideration as I shall point out in more detail later.

If one assumes that the outgrowth from the oögonium in *Sphaerotheca* represents simply a large, well-nourished ascogenous hypha, then a perfect type of crosier occurs here also. The ascus, according to Harper (52), is formed from the binucleated penultimate cell of this outgrowth (FIG. 8, A). Uninucleated ultimate and antipenultimate cells are regularly formed.

A few forms have been reported in which it is claimed that the ascus arises directly from the end cell of the ascogenous hypha without any bending over of the terminal portion. Maire (60) describes such a process in *Galactinia succosa*. The asci of *Penicillium* are described by Brefeld (16) as arising in rows from cells of the ascogenous hyphae. The same is true for *Exoascus* (Dangeard, 31). Thaxter (88) and Faull (39) have described the formation of the asci from the egg in several species of the Laboulbeniaceae. Here the ascogenous cell buds out directly into a large number of asci. Faull suggests several possible homologies for the cells developed from the germination of the egg, but he by no means makes clear their relationships to the parallel stages in the red algae.

Ramlow (73) points out that the ascus in *Thelebolus* arises directly from a large binucleated cell of the ascogonium the other cells of which are uninucleated. In some cases the ascogenous cell is the subterminal cell.

H. B. Brown (18) has recently reported that the asci of *Xylaria* are simply outgrowths from the end cells of the much-branched ascogenous hyphae. His description is however very brief and should perhaps not be quoted as proof of a departure from the general method of ascus formation.

Dangeard's (31) separation of the Ascomycetes into two groups, the so-called "rectascées" and "curveascées," is not supported by the observations of Fraser and Chambers (46), Dale (29, 30), Brooks (17), and Blackman and Welsford (12), who report the

formation of the crosier in such forms as *Aspergillus*, *Gymnoascus*, *Gnomonia*, and *Polystigma*.

A number of cases have been reported where the end cell bends down and fuses with the cell below the ascus, so that in this way a new cell is formed containing two nuclei which may later fuse and form a new ascus. W. H. Brown (19, 20) noted such cases in *Leotia*, *Geoglossum*, and *Lachnea scutellata;* Fraser (43) in *Humaria rutilans;* and Claussen (26) in *Pyronema*.

The relations of the outgrowths of the egg in those red algae in which secondary fertilizations occur to the so-called auxiliary cells have been the subject of extensive study since the time of Schmitz, and there yet remain many unsolved questions both as to the position and morphological character of the auxiliary cells and the cytological features of the fusion of the egg outgrowths with them. Schmitz called these filaments proceeding from the fertilized egg oöblastema filaments. They are to be distinguished from the gonimoblasts which produce spores directly. Their general resemblance to ascogenous hyphae is certainly striking, as Oltmanns (68) pointed out, and it is strange that it has not been more specifically discussed. Both are outgrowths of the fertilized egg or its equivalent. Schmitz made clear their nature and method of development in the red algae, but Oltmanns claims that Schmitz was mistaken in his interpretation of the fusions of the oöblastema filaments with the auxiliary cells as repeated sexual processes.

Schmitz's classification of the Florideae based largely on the morphology of their reproductive organs at once superseded the older systems of Nägeli (62) and Agardh (1). Daines (28), a pupil of Setchell, has analyzed the data upon which the present classification is based and describes very briefly and clearly the characters of the different groups as generally accepted to-day. There are five main groups:—Nemalionales, Gigartinales, Rhodymeniales, Ceramiales, and Cryptonemiales.

In Schmitz's simplest group are found the well-known forms *Batrachospermum*, *Nemalion*, etc. In these forms vegetative envelopes for the mass of carpospores are almost or entirely wanting (FIG. 6, A). The sporogenous cells, gonimoblasts, grow out from the fertilized egg as short filaments which become septate and give rise at once and without secondary fusions to masses

of carpospores. In certain species, such as *Dermonema dichotomum* (Schmitz 81), the sporogenous filaments form a complex system which develops wholly within the thallus, producing numerous clusters of carpospores separated by sterile tissue (FIG. 6, B). There can be no question in these forms as to the essential facts of their sexual reproduction. It has been described in *Nemalion* (Wolfe, 93) and in *Batrachospermum* (Osterhout, 69). The spermatium nucleus penetrates the trichogyne and passes down to the carpogonium where it unites with the egg nucleus.

The remaining four groups, Gigartinales, Rhodymeniales, Ceramiales, and Cryptonemiales, in which a conjugation between the outgrowths of the carpogonium and an auxiliary cell occurs, do not differ materially among themselves for the purposes of our discussion, except perhaps as to the time and place of the development of the auxiliary cell, this cell being most closely connected with the carpogenic branch in the Gigartinales, while in the Ceramiales it may be entirely independent of, but paired with, the branch which bears the egg cell. In the former we have a secondary fusion of a very simple type. Sturch (87) has described the formation and development of the procarpic branch of *Harveyella mirabilis*. This species is parasitic upon one of the larger red algae and is interesting to us because of its lack of chlorophyll. The curved carpogenic branch is composed of four cells and a basal cell which functions as an auxiliary cell. This is a large cell well supplied with nourishment. After fertilization and after the trichogyne has been cut off by a septum, as claimed by Sturch, the carpogonium grows out into a slender filament which unites with the auxiliary cell below, and from this a central cell is formed which gives rise to sporogenous hyphae (FIG. 4, E). The process in such a case in which the cells below the egg become involved by secondary fusions in the development of a spore fruit may be more similar to that in the lichens, *Ascobolus carbonarius*, etc., where we have the ascogenous hyphae developing from cells far back from the trichogyne, than has hitherto been supposed. The breaking down of the cross walls of the ascogonium in the lichens (Baur, 8, 9; Darbishire, 32; Bachmann, 3) and the formation of pores in the cross walls in the ascogonia of *Ascobolus* (Harper, 50), *Ascophanus carneus* (Cutting, 27), and *Lachnea cretea* (Fraser, 44),

may have the same significance as the development of the egg outgrowth and its fusion with the basal cell or cells of the procarpic branch in such forms as *Harveyella*, *Dudresnaya coccinea* (FIG. 5, E), *Polyides*, and *Erythrophyllum* (FIG. 4, C, D). This topic will be referred to further below.

In *Wrangelia* (Zerlang, 98) the outgrowth from the carpogonium appears to be a sac-like structure connecting with the basal cell of the procarpic branch and forming the so-called central cell from which the sporogenous filaments arise.

In many species of the red algae the lower cells of the procarpic branch become involved in extensive cell fusions which follow fertilization. This is well shown by Twiss (91) for *Erythrophyllum delesserioides* which, as he points out, is one of the Gigartinaceae. The procarpic branch consists of seven or eight cells, the lower three of which are very large, considerably elongated and well nourished. Above these are three much smaller cells but of about the same shape, while the next cell is minute and triangular, and is connected with the carpogonium by a coiled slender portion. After fertilization, presumably, the oöblastema filament grows out and connects with the lowest of the three large cells, which is the auxiliary cell (FIG. 4, C). Then occur the intimate fusion of all three cells and the giving off of gonimoblast filaments from all parts of this fusion cell (FIG. 4, D), very much as in the lichens (FIG. 7) and certain other Discomycetes (37, 44, 27), as just noted, where several cells of the ascogonium become connected by pores in the cross walls and ascogenous hyphae arise from the portions corresponding to each of the original cells. In *Erythrophyllum*, *Gigartina*, and other members of the Gigartinaceae the sporogenous hyphae form an extensive branching system penetrating the thallus so that a somewhat spherical swollen spore fruit is finally developed, perhaps corresponding to such an ascocarp as that of *Penicillium*.

It is a striking and characteristic fact for both the Ascomycetes and red algae that in these cases the spore-bearing filaments should arise from several rather than one cell, and that these cells are connected by pores in the one case and oöblastema filaments in the other. Ascogenous hyphae, gonimoblasts of the *Batrachospermum* type, oöblastema filaments, and even those fusions between

cells of the ascogonium are all to be considered morphological equivalents arising by reduplication at different stages out of some primitive type of egg outgrowth such as we find in the gonimoblasts of *Nemalion*.

Phillips (72) has shown that the cystocarp formation in a number of species of the Rhodymeniales differs from that in the Gigartinales in that the auxiliary cell is derived from the basal cell of the carpogenic branch or is its sister cell. The conjugating tube or outgrowth from the carpogonium is very similar to that found in *Harveyella*.

Yamanouchi (97) has described in some detail the development of the fusion cell in *Polysiphonia* by the union of the auxiliary cell with the basal cells of the carpogenic branch and other adjacent sterile cells. He claims that the union between the carpogonium and the fusion cell takes place by means of a specially formed connecting "auxiliary" cell. In the Gigartinales and Rhodymeniales the carpogenic branch is so curved over as to bring the carpogonium into the near neighborhood of the auxiliary cell.

In *Callithamnion*, a type of the group Ceramiales, the entire process of fertilization and the secondary fusions between the carpogonium and the auxiliary cells has been studied by Oltmanns (68). Paired auxiliary mother-cells are formed on either side of the main axis. One of the mother-cells divides, the lower portion giving rise to the short procarpic branch. At the same time a basal cell is cut off from each mother-cell, leaving the auxiliary cells above (FIG. 5, A). After fertilization the carpogonium grows out into two short oöblastema filaments each of which unites with an auxiliary cell carrying over a daughter nucleus of the fertilized egg. The auxiliary cell now contains two nuclei, the original auxiliary cell nucleus and a daughter nucleus of the fertilized egg. Cell division takes place cutting off the auxiliary cell nucleus below, leaving only the descendant of the egg above (FIG. 5, B), from which the sporogenous filaments are developed. The nuclei of the auxiliary cells degenerate without taking any part in spore formation.

A very simple and clear description of cystocarp formation in *Prionitis Lyallii* has been given by Daines (28). The curved, five- or six-celled carpogenic branch is entirely imbedded in the

thallus through which the trichogyne penetrates to the surface (FIG. 4, F). The auxiliary cell is derived from the lower cell of one of the sterile filaments and is brought into connection with the carpogonium by a short oöblastema. Daines was unable to discover that this filament united with any other cell as in the case of other species of the Grateloupiaceae described by Berthold, and since procarpic branches and auxiliary cells are borne in pairs Daines concludes that this species should be placed with the Ceramiales.

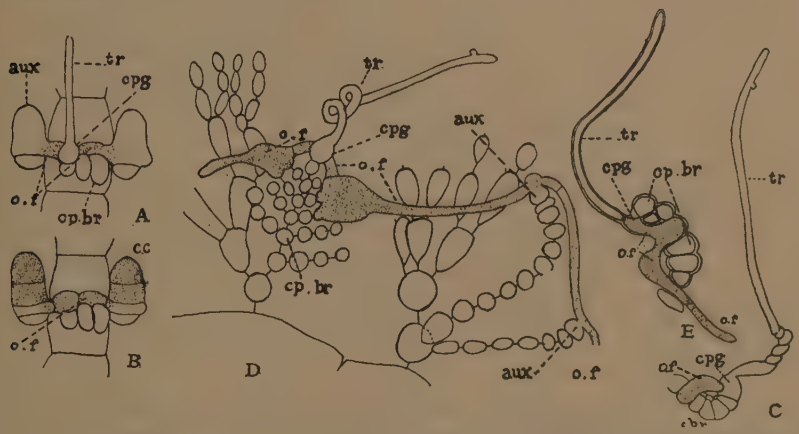

FIG. 5. Trichogynes and outgrowths from the carpogonium in the red algae. A, B. *Callithamnion corymbosum;* C, D. *Dudresnaya purpurifera;* E. *Dudresnaya coccinea. aux,* auxiliary cell; *cp.br,* carpogenic branch; *cpg,* carpogonium; *o.f,* oöblastema filament; *tr,* trichogyne. A, B, D, E, Oltmanns; C, Schmitz.

Vastly more complex and perhaps furnishing still more evidence as to the ancestry of the Ascomycetes are the Cryptonemiales, the forms upon which Schmitz based his theory of secondary sexual fusions.

The procarpic branch in *Cruoriopsis cruciata* (Schmitz, 78, 80) is imbedded within the thallus but its trichogyne extends out beyond the surface. Near these procarpic branches other filaments are developed which Schmitz called "procarps without trichogynes." The end cells (auxiliary cells) of these branches remain imbedded in the thallus and do not grow out into trichogynes. After the fertilization of the procarp there now grows out from its under part an oöblastema filament which branches freely and spreads widely inside of the thallus and "fertilizes the procarp

of the second sort" by fusing with the end cell. These same oöblastema filaments then go on to other procarps of the second sort. Each of these "fertilized" auxiliary cells sends out only one or two rows of from two to four carpospores. Oltmanns (67) says only one simple two- to four-celled spore chain arises from each of these secondary fusions, and we thus have a very interesting parallel to the conditions in the ascogenous hyphae, where from each vegetative nuclear fusion a single ascus results with typically eight spores.

Among the Cryptonemiales Schmitz notes interesting minor differences in the manner in which the auxiliary cells develop after the secondary fusion. In *Dudresnaya* (FIG. 5, C, D), *Polyides*, *Petrocelis*, etc., after fusing with the distant auxiliary cell the oöblastema filament becomes cut off from it and the sporogenous cells arise from the part corresponding to the section of the oöblastema cell. Schmitz saw no nuclear fusions here, and each cell seems to maintain its individuality in a large degree. In *Calosiphonia* the contents of the oöblastema cell go over to the auxiliary cell. Here the outgrowths or gonimoblasts giving rise to the spores arise from the portion originally belonging to the auxiliary cell. In this second case Schmitz believes that the nucleus of the oöblastema cell goes over to the auxiliary cell, but he could have seen no real movement. In *Gloiosiphonia* the entire cell contents of the oöblastema cell except the plasma membrane pass over into the auxiliary cell. There is an intimate fusion of the cytoplasms, and in this case Schmitz believes that the two nuclei unite in what he calls the "second sexual process." He describes the protoplasm of the oöblastema cell as moving over and combining intimately with that of the auxiliary cell, leaving the other empty except for the plasma membrane, and in this case believes that a nuclear fusion actually occurs. Oltmanns denies that there are ever any nuclear fusions here, but he figures the oöblastema cell as empty and holds that the protoplasm and nuclei pass to the auxiliary cell.

Schmitz may be wrong; the next step, however, in the developmental stages which he describes would be the fusion of the nuclei, and with a nuclear fusion under such conditions we should have a further point of resemblance to the young ascus.

It is not impossible that in these secondary cell fusions we should seek for an explanation of the puzzling vegetative nuclear fusions in the ascus. The reported fusion between the end cell of the ascogenous hypha and the cell just below the ascus would perhaps serve the same purpose as would the fusion of the end cell of the oöblastema filament with some other cell of the procarpic branch in case no auxiliary cell were available. Since Oltmanns (68) confirms Schmitz's account as to the cell fusions in *Dudresnaya* and *Gloiosiphonia* the facts here may be taken as fairly well established. His further claim that the nucleus of the auxiliary cell in *Dudresnaya*, *Callithamnion* and *Gloiosiphonia* degenerates, as noted above, after having taken a position as far away as possible from the oöblastema nucleus certainly needs further confirmation. Oltmanns' figures are quite diagrammatic and the successive stages in the disintegration of the vegetative auxiliary cell nucleus are not represented at all. The division stages also by which the fertilized egg nucleus is claimed to multiply and furnish daughter nuclei for further growth are not shown. It is to be remembered that the disintegration of a nucleus and the taking of its cytoplasm by another nucleus as claimed by Oltmanns is entirely without analogy elsewhere in connection with fertilization processes either in the plant or animal kingdom. We certainly need more evidence as to the nuclear phenomena occurring in connection with these secondary fertilizations of Schmitz and the possibility that we shall here find the explanation of the nuclear fusions in the ascus is surely worth considering.

The obvious similarities between ascocarps and cystocarps have doubtless been the most common ground for assuming a relationship between the Ascomycetes and the Florideae. As noted above Schmitz did not consider the form of the mature cystocarp as having great phylogenetic significance. In each of the main divisions of the red algae as we now understand them we find considerable variation in the characters of the fruit body. In the Nemalion group for example we find all stages from the completely unprotected glomerulus of carpospores without sterile filaments (FIG. 6, A) up to well-formed cystocarps with surrounding protecting hyphae. In *Scinaia* (FIG. 6, C) the cystocarp corresponds in form and method of development to a typical pyreno-

carpic fruit body. The protective envelope is developed from the outgrowths from the basal cells of the carpogenic branch. *Wrangelia* is another comparatively simple type but the interpretation of its cystocarp may be open to question. The gametophytic protective filaments are quite definitely disposed about the masses of carpospores. The large and complex carpospore fruits of *Gigartina*, *Erythrophyllum*, etc., the so-called nemathecia, may be regarded as cleistocarpic and, as noted, may correspond to the ascocarp in *Penicillium*. Such nemathecia are found in the com-

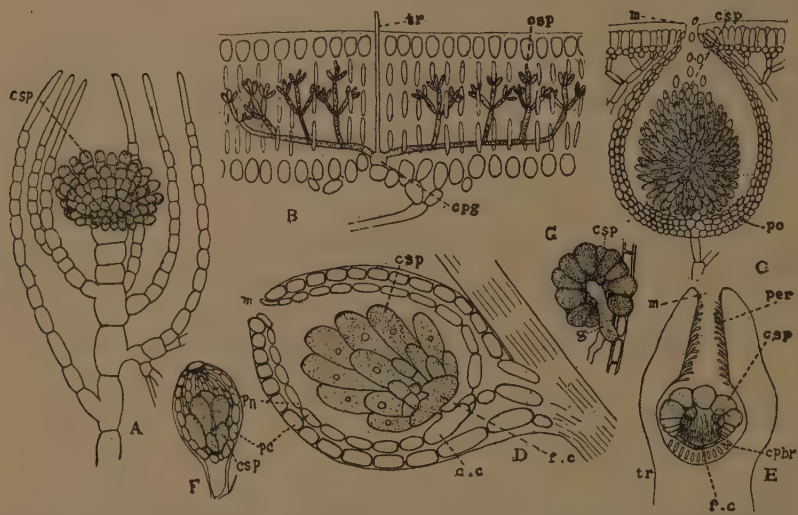

FIG. 6. Cystocarps of red algae. A. *Nemalion multifidum;* B. *Dermonema dichotomum;* C. *Scinaia furcellata;* D. *Polysiphonia;* E. *Corallina mediterranea;* F. *Lejolisia;* G. Spore group, *Polyides*. *c.c*, central cell; *cpg*, carpogonium; *csp*, carpospore; *f.c*, fusion cell; *pc*, enveloping filaments or pericarp; *pn*, paranemental filaments or paraphyses; *m*, opening of cystocarp; *per*, periphyses; *tr*, trichogyne. A, Farlow; B, C, Schmitz; D, Phillips; E, Solms-Laubach; F, Bornet; G, Thuret.

paratively simple as well as in the highest groups of the red algae. The conceptacle of *Corallina* (FIG. 6, E) is a structure presumably formed before the development of the procarpic branches, and can not perhaps properly be compared with the ascocarp of the Ascomycetes.

It has been assumed, probably without sufficient grounds, that the cleistocarp is the primitive ascocarp of the Ascomycetes, because in the great majority of cases so far as now known the

ascocarps are in their younger stages more or less closed structures. Practically all authors have made the characters of the ascocarp the basis for subdividing the group, though E. A. Bessey (11) accepts the results of Miss Bachmann's work as further evidence of the possible primitive character of *Collema*, and C. E. Bessey (10) has rearranged his classification of the Ascomycetes placing the "Discolichens" with the Laboulbeniales as transition groups connecting the Ascomycetes and the red algae.

Persoon (71) distinguished between angiocarpous and gymnocarpous forms of fungi. *Mucor*, *Scleroderma*, *Thelebolus*, and *Tuber* are "Angiocarpi," and *Phallus*, *Agaricus*, *Boletus*, *Helvella*, *Ascobolus*, and *Tremella* are "Gymnocarpi." Fries (47, 48) distinguished between the Pyrenomycetes and Discomycetes by the characters of the hymenial layer and the form of the mature fruit. He did not concern himself with the morphology and development of the early stages of the ascocarp as did De Bary (6) who realized that many Discomycetes have entirely closed fruit bodies in their younger stages. *Ascobolus furfuraceus* is the familiar example of this sort of ascocarp (FIG. 9, B). De Bary emphasized the fact that the form of the mature fruit is not a final proof of relationship. The gymnocarpous forms may become cleistocarpous or vice versa. De Bary was uncertain whether the primitive Ascomycetes had closed or open ascocarps and did not regard the method of development in *Ascobolus* as proof of the primitive character of the cleistocarp.

Brefeld (16) held that all ascocarps are cleistocarpous in their youngest stages. Schroeter (82) divided the Ascomycetes into three groups accordingly as they are gymnocarpous from the first, *Pyronema*, *Helvella*, etc.; or first closed, then later opening up, Pezizaceae in general; and third, the more or less permanently closed Pyrenomycetes. In recent years more attention has been paid to the actual form of the youngest obtainable fruits. Fischer (42) and Bucholtz (22–24) have studied a number of the Tuberineae and find that in many cases the hymenium is at first exposed and only later becomes closed over by the infolding of the peridium.

Dittrich (35) and Durand (38) find that certain Helvellineae are cleistocarpous at the time the hymenium is being organized.

In certain species of *Lachnea*, as noted above, the hymenium is at no time enclosed by the peridium. All these observations are quite contrary to the views that have been commonly held. The significance of the rather delicate weft of hyphae covering the hymenium of *Geoglossum*, *Mitrula*, *Spathularia*, *Microglossum*, *Cudonia*, etc., according to Dittrich and Durand, can not be regarded as entirely clear and the question whether the ascocarps in these cases are cleistocarpous at first can only be settled by further study of

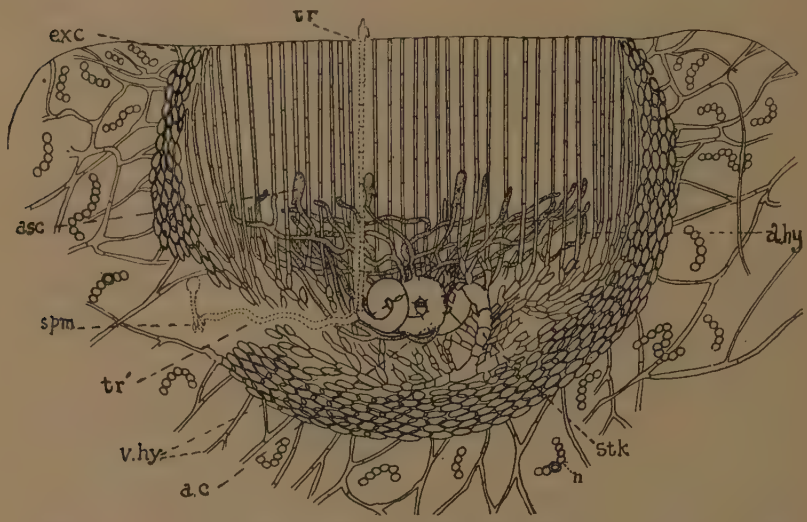

FIG. 7. Apothecium of the Collemas showing the difference between the trichogynes of *C. microphyllum* and those of *C. pulposum*. The trichogyne, *tr*, of *C. microphyllum*, represented by dotted lines, is perpendicular to the surface of the thallus; the trichogyne, *tr'*, of *C. pulposum*, also represented by dotted lines, lies more or less horizontally in the thallus. The figure shows that paraphyses arise from the vegetative hyphae, *v.hy*, as well as from the stalk, *stk*, of the ascogonium and that ascogenous hyphae, *a.hy*, arise from several cells of the ascogonium which are connected by broad pores in the cross walls. *a.c*, ascogenous cells; *asc*, ascus; *exc*, excipulum; *n*, *Nostoc* colonies; *spm*, spermatia; *stk*, stalk of ascogonium. After Stahl, Bachmann, and others.

earlier stages. The real question as to whether an ascocarp is to be classed as open or closed in its early stages depends on whether the young hymenial layer arises endogenously as in *Ascobolus furfuraceus* (FIG. 9, B), or is from the first free and exposed as in *Pyronema* (FIG. 11, B).

Authors have commonly recognized at least four types of

ascocarp: (1) the typical angiocarp or cleistocarp of Schroeter's Plectascineae with no hymenial layer or paraphyses in parallel arrangement, and the perithecium of the Erysiphaceae (FIG. 8, A) which bursts irregularly; (2) the discocarp or apothecium, the type commonly supposed to be possessed by most Discomycetes, for example, the well-known fruit body of *Ascobolus furfuraceus* (FIG. 9, B) where the hymenium is at first entirely closed over and is later exposed by the expansion of the asci and growth of the paraphyses; (3) the pyrenocarp of the vast majority of Pyrenomycetes typically provided with an ostiole through which the spores are expelled (FIG. 8, C); (4) the true gymnocarp, such as that of *Ascodesmis*, *Pyronema* (FIG. 11, B), *Ascobolus magnificus* (FIG. 11, A), *Lachnea stercorea* (FIG. 10), *L. scutellata*, and the Exoasci.

The use of such terms as angiocarpous, pseudo-angiocarpous, hemi-angiocarpous, etc., has come to be quite loose. As noted, Persoon (71) divided the fungi into two groups on the basis of the form of the mature fruit. De Bary and other morphologists of his time extended the use of the term angiocarp to those immature fruit bodies in which the hymenial layer is covered by a peridium. The term angiocarp, or cleistocarp, has long been used to distinguish the closed type of fruit in various classes of plants, and the older writers from Persoon on describe fungi in which the hymenium is enclosed by a peridium or rind as angiocarpous. As it is always possible to determine whether the asci (and paraphyses, if present) arise endogenously this use of the term is perfectly clear and should be maintained. The distinction between cleistocarpic, discocarpic, and gymnocarpic must be based on the method of origin of the hymenial layer rather than merely on the question as to the envelopment of the ascogonium. Most ascogonia are very soon more or less covered by enveloping hyphae. The real distinction lies between such forms as *Ascobolus furfuraceus* (FIG. 9, B) in which the hymenial layer arises endogenously, and *Pyronema* and *Ascobolus magnificus* (FIG. 11, A) in which it is from the first superficial and exposed. To ignore the question of the exogenous origin of the hymenium in the case of those Ascomycetes in which the ascogonium has been described as enclosed in its very early stages, is without any morphological

justification. Even though the ascogonium be completely enclosed at first, if the hymenial layer subsequently develops superficially the ascocarp must certainly be described as discocarpous and not properly cleistocarpous at any stage. Illustrations of permanent cleistocarps are the well known types *Sphaerotheca*, *Chaetomium fimeti*, *Aspergillus*, *Elaphomyces*, etc. Illustrations of those that are gymnocarpous and then become closed are *Tuber excavatum*, *Balsamia* (FIG. 8, D), *Choiromyces*, and *Hydnocystis*.

Two types of cleistocarps have been distinguished. We may take the mildews as well known cases of the first type whose method of development has been fairly clear since De Bary's time. The sporophyte proper which develops from the fertilized egg remains enclosed in a gametophytic envelope, the perithecium (FIG. 8, A), which finally bursts irregularly when the spores are ready to germinate. The second type of cleistocarp, which is open at first but later becomes closed by the growth of the peridium (FIG. 8, D), has been carefully investigated by Fischer (42) and Bucholtz (22–24). In a number of the Tuberineae at the time when the hymenium is first recognizable as such it is freely exposed to the exterior. Later by a process of infolding and the active growth of a peridium it becomes entirely enclosed. Bucholtz (23) believes that the mature form of the fruit body, for example, whether it is angiocarpous or gymnocarpous, is in a great measure determined by the environment and is not a basis for determining phylogeny. Bucholtz calls this second type of cleistocarp "pseudoangiocarp" and proposes to use the term "hemiangiocarp" to distinguish the abnormal forms of *Tuber puberulum* where in rare cases the young hymenium is entirely covered at first by a very delicate weft of hyphae which extends out from the peridium proper. He agrees with Dittrich and Durand that any Discomycete in which the ascogonium is enveloped by sterile hyphae is in its ontogeny in fact cleistocarpous, yet in his treatment of the Tuberineae he entirely ignores the possibility that ascogonia may yet be found in them which are surrounded at an early stage by a layer of enveloping hyphae, and classes such forms as *Tuber excavatum* as gymnocarpous, or pseudoangiocarpous, as he prefers to call them. As I have noted it is of little importance whether or not the ascogonium is enveloped in its

early stages providing the asci and hymenium develop superficially, as he claims is the case in certain of these hypogaei (FIG. 8, D).

In spite of the vast amount of work that has been done by Woronin, Fisch, Frank, Gilkinet, Kihlman, Oltmanns, Nichols, and others on the origin and morphology of the pyrenocarp it is not clear just how the ostiole originates. These authors give us no concise account of this feature. We find in the Pyrenomycetes forms like *Chaetomium fimeti* which are permanently cleistocarpous as well as the great mass of forms which have a characteristically developed ostiole, and the conditions here are parallel

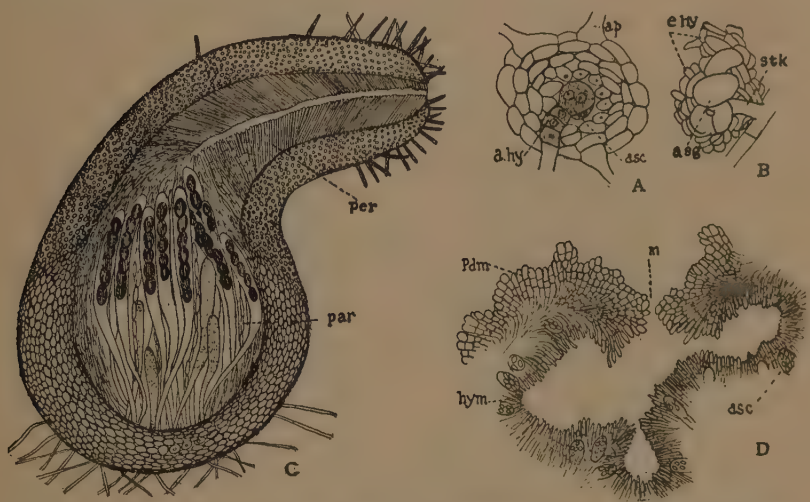

FIG. 8. Ascocarps of Ascomycetes. A. *Sphaerotheca;* B. Young stage of *Melanospora parasitica;* C. *Sordaria fimiseda;* D. *Balsamia.* *a.hy*, ascogenous hyphae; *asg*, ascogonium; *ap*, appendages; *e.hy*, enveloping hyphae; *m*, opening of the fruit body; *par*, paraphyses; *per*, periphyses; *stk*, stalk. A, Harper; B, Kihlman; C, Woronin; D, Bucholtz.

in an interesting way to those in *Ascobolus*, where we have forms like *A. furfuraceus* which is at first cleistocarpous and later becomes wide open, and other forms like *A. magnificus* which is a discocarp from the start. The development of the pyrenocarp has been followed out by Kihlman (57) in *Melanospora*, by Oltmanns (66) in *Chaetomium*, and by Miss Nichols (64) in *Hypocopra* and *Ceratostoma*, and we know that in these forms some sort of a primordium or

ascogonium is present and that these primordia are completely surrounded by a closely packed layer of enveloping hyphae (FIG. 8, B), but this does not at all settle the question as to how the ostiole originates or even whether the hymenium is endogenous in its origin. Miss Nichols says that the ascogonium of *Ceratostoma* gives rise by cell division to a mass of cells from which asci finally develop, and that the ostiole results from the schizogenetic rupture of the wall at the papillate apex. The interesting account of the development of the ostiole in the region of the base of the archicarp as given by Kihlman for *Melanospora* needs confirmation. According to this account the opening of the ascocarp is at a point which in all other cases is at the center of its base.

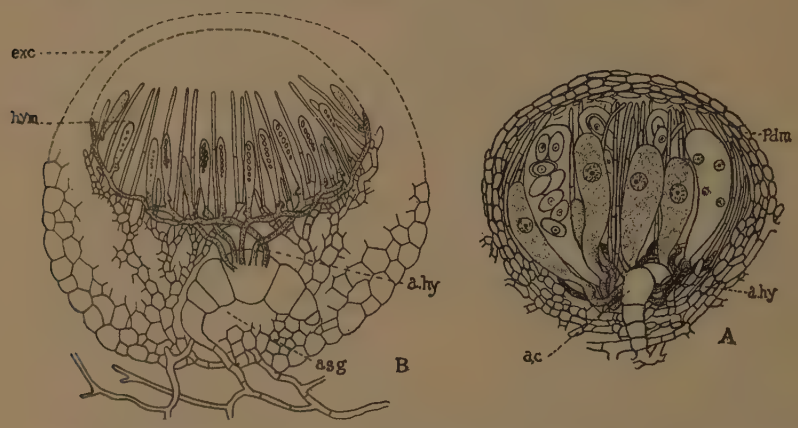

FIG. 9. Discocarps of *Ascobolus*. A. *Ascobolus Winteri;* B. *A. furfuraceus*. *a.c*, ascogenous cell; *asg*, ascogonium; *a.hy*, ascogenous hyphae; *exc*, excipulum; *hym*, hymenium; *pdm*, periderm. A, original; B, adapted from Sachs.

Two types of apothecia have also been commonly recognized. First, those like *Pyronema* (FIG. 11, B), in which the hymenium is exposed from the beginning; and second, those like *Ascobolus furfuraceus*, in which the hymenium originates endogenously and later becomes exposed by the bursting of the apothecial envelope (FIG. 9, B). The method of the development of the apothecium of *Pyronema* as representing the first type is certainly well known. No excipulum is formed and the paraphyses and asci form a uniformly superficial naked layer (FIG. 11, B). *Ascodesmis nigricans* is an even more simple and open type of fruit body. The apothecium of

Lachnea stercorea (Fraser, 45) is at no time cleistocarpous, although Miss Fraser does describe and figure sterile hyphae enclosing the lower part at least of the ascogonium. The hymenial layer is however exposed from the first (FIG. 10). *Lachnea scutellata* (W. H. Brown, 20) evidently develops along much the same lines judging from Brown's figures and description, "when the hymenium is first formed it is covered by the younger setae of the cortex . . . ."

Ascobolus magnificus is a further example of the first type. I have already briefly described this species (36) from material grown on the natural substratum and it has since been cultivated on artificial media for several months where the structures giving rise to the apothecium have been more carefully investigated. Although it does not always fruit abundantly in these cultures still a large number of primordia have been obtained and many apothecia have been grown to maturity. The stages passed through give an excellent illustration of a type in which the hymenium is never fully enclosed. The young fruits lie directly on the surface of the agar where they may be carefully studied and I have had no difficulty in arriving at a positive conclusion that in every normal case the ascogonium is prolonged into a rather thick septate trichogyne whose end cells come down over or coil about the end of a club-shaped antheridium which is provided with a stalk of variable length, usually one to three cells. I was not able to make out the antheridium in my earlier studies on specimens gathered in nature. The archicarp and antheridium as far as I have been able to determine do not arise from the same hypha but from hyphae either running along parallel or crossing at an angle much the same as De Bary and Harper found in the mildews. In several cases two functional ascogonia were seen in sections of young apothecia but I suspect that these are merely accidentally included in the same fruit body. Several cases have been observed also where two ascogonia lie exposed close together on the surface of the agar and I have seen not uncommonly two or three additional non-functional antheridia growing near the young fruits.

The ascogonium is exceedingly large, rising upward above the surface of the agar in its younger stages, and if undisturbed is found maintaining a somewhat vertical position in the young apothecium. It not infrequently happens that the ascogonium falls over on the

antheridial branch so that it is not always possible to determine the exact origin of the antheridium and it may possibly in some cases arise from the same hypha that produces the ascogonium. The trichogyne is sharply differentiated from the ascogonium and is not merely a tapering elongation of it such as is found in *Ascobolus Winteri* and *A. immersus*. It is more nearly like Miss Fraser's figure of *Lachnea stercorea* (FIG. 10). It is usually composed of about seven or eight cells, the end cell being much longer, and curved about the antheridium. FIG. 11, A, gives one an idea of the general arrangement and relationships of the ascogonium, trichogyne, antheridium, and the parent hyphae. The "enveloping hyphae" arise almost entirely from the mycelial hyphae on either side of the ascogonium and antheridium and not merely from the stalk of the ascogonium as they do quite exclusively in *Ascobolus Winteri*. Ascogenous hyphae begin to grow out of the ascogenous cell sometimes even before any "enveloping hyphae" have made their appearance and at no time are the primordia and the ascogenous hyphae completely surrounded by a peridial layer. Paraphyses, "enveloping hyphae" and ascogenous hyphae grow upward together. The apothecium is entirely similar to *Pyronema* in this respect. FIG. 11, A, is a somewhat diagrammatic representation of a young apothecium. It will be perceived by a comparison of FIG. 10 of *Lachnea stercorea* and this figure of *Ascobolus magnificus* that these two species are very similar indeed except for the colored spores of the *Ascobolus* and the hairs on the apothecium of the *Lachnea*. Their sexual reproduction and the development of the apothecia differ in no important particular. As noted Brown's figures of a young apothecium of *Lachnea scutellata* show that this species develops in the same way.

The behavior of the sterile or enveloping hyphae in forming the apothecium of *Ascobolus magnificus* is quite different from what it is in *A. furfuraceus*, and resembles more nearly what takes place in *Lachnea stercorea*. The archicarp is considerably raised above the surface of the medium by its long stalk very much as are the archicarps of *Pyronema*. The first growth of "enveloping hyphae" is seen to take place about the time the ascogenous hyphae make their appearance as papillae on the ascogenous cell. Sterile hyphae

arise from the parent hyphae of both sex organs, as well as from the stalk of the archicarp. I have not found that the stalk of the antheridium gives rise to any enveloping hyphae. At first these sterile hyphae grow upward from all sides of the ascogonium. They are very coarse strands which branch profusely, some scattering branches wandering up and over the trichogyne and ascogenous cell, but at no time is there a weft or layer of hyphae completely surrounding the ascogenous cell such as is formed in *Ascobolus furfuraceus*, *A. carbonarius*, etc. The inner branches of the enveloping hyphae give rise to the paraphyses. I have been able to trace connections between the enveloping hyphae that arise

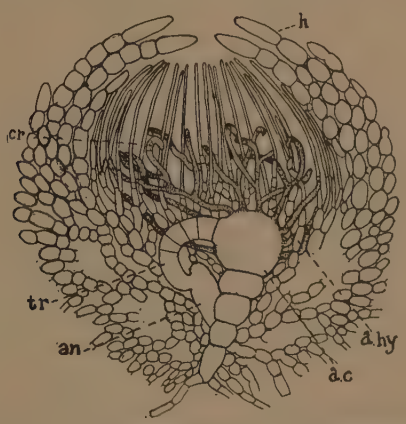

FIG. 10. Gymnocarp of *Lachnea stercorea*. *a.c*, ascogenous cell; *a.hy*, ascogenous hyphae; *an*, antheridium; *h*, hairs; *par*, paraphyses; *cr*, crosier; *tr*, trichogyne. After Fraser.

from the parent mycelial hyphae and the paraphyses in many cases, but I believe that many paraphyses likewise arise from the branches of the ascogonium stalk. In sections of young apothecia just visible without a lens we find immediately above the ascogenous cell a number of somewhat parallel hyphae running vertically upward. Some of these are ascogenous hyphae, others are paraphyses or hyphae which have pushed in among the ascogenous hyphae and which by further branching will give rise to paraphyses. The two kinds are easily distinguished by the larger nuclei of the ascogenous hyphae and the fact that in sections 10 μ or more thick the ascogenous hyphae are easily

traced back to the ascogenous cell. There is at this time (FIG. 11, A) no perithecial layer such as is to be found in *A. furfuraceus* at such a stage. The outer hyphae are now becoming more compact and some of them begin to grow inward forming what in appearance is an inrolled margin, covering in part the hymenial layer which as I have stated is visible from the first and remains exposed throughout the development. The narrowness of the opening above the hymenium at this time led me to erroneously describe the young fruit as "at first closed, then opening by a pore" (36). Microtome sections and careful examination of large numbers of specimens grown on the surface of agar media in plate cultures have made it clear that the hymenium is never closed over; in fact the ascogonium is not more "protected" than are

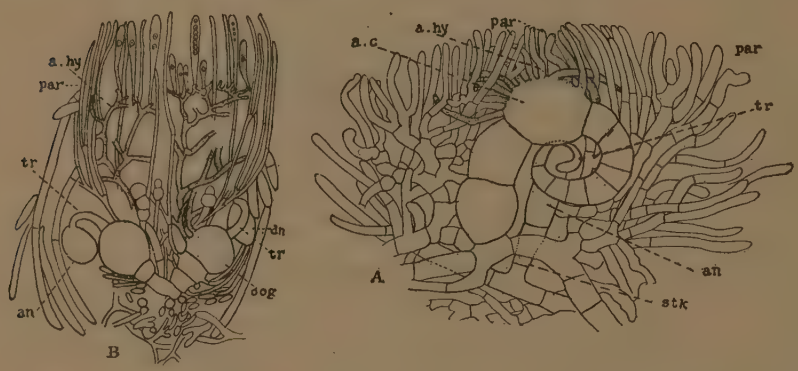

FIG. 11. Gymnocarps. A. *Ascobolus magnificus;* B. *Pyronema confluens.* *a.c,* ascogenous cell; *a.hy,* ascogenous hyphae; *an,* antheridium; *oog,* oögonium; *par,* paraphyses; *stk,* stalk; *tr,* trichogyne; A, original; B, Harper.

the ascogonia of *Pyronema.* Sections of older apothecia show that there is a well-developed sterile margin, the "excipulum," the outer cells of which strongly refract the light thus making a beautiful snow white margin which is inrolled at first (FIG. 12) but later as the hymenium broadens becomes expanded or even reflexed (FIG. 13).

The second type of apothecium which is at first closed and later opens is illustrated by the familiar figures of *Ascobolus furfuraceus.* Not only is the ascogonium entirely enclosed at an early stage but the young hymenial layer is completely covered by

a well-developed layer of pseudoparenchymatous cells. The growth of the asci and the pushing out of the paraphyses break this layer above the hymenium irregularly and this sterile portion is forced back and becomes the excipulum of the apothecium (FIG. 9, B).

Lachnea cretea (Fraser, 44) and *Lachnea abundans*, which I have had the opportunity to study in artificial cultures for some time, are entirely enclosed or cleistocarpous in their younger stages and are only opened by the thrust of the paraphyses upward as in the case of *Ascobolus furfuraceus*. My sections of the young apothecium of *Ascobolus Winteri* (FIG. 9, A) and of *A. Leveillei* show that the hymenium is well covered by a solid wall of hyphae. Even in stages when the spores of some asci are nearly mature this wall is still unbroken and it appears that the asci themselves in their elongation may be the chief agency in bursting open the ascocarp, especially in *A. Winteri*. In this species the ascogonium lies well down at the bottom of the apothecium (FIG. 9, A). The ascogenous hyphae grow out from only one cell of the ascogonium as rather thick short hyphae.

W. H. Brown's figures of young fruit bodies of *Lachnea scutellata* certainly indicate that in this species the hymenium is slightly exposed from the first. His diagram shows that the inner branches of certain hyphae produce the paraphyses, while the outer branches of these same sterile hyphae are prolonged into the hairs which fold in over the hymenium in younger stages. Bucholtz describes what I take to be very much the same condition for *L. leucotricha*, although he claims the young fruit is angiocarpous on account of the extremely delicate weft of hyphae that surrounds the whole fruit in its earlier stages. *Lachnea stercorea* (FIG. 10) as described by Miss Fraser is gymnocarpous from the first. Miss Fraser states that the ascogonium is enclosed by enveloping hyphae although the young hymenium is not. Her figures show only the stalk of the ascogonium surrounded by sterile hyphae. *Sphaerosoma* may prove to be gymnocarpous at first, although there seems to be a lack of complete agreement in the descriptions of this form by Rouppert (74), Setchell (84), and Seaver (83).

In *Ascobolus Winteri* it is only rarely that any enveloping hyphae arise from the mycelial hyphae giving rise to the asco-

gonium. All sterile hyphae, paraphyses and secondary mycelium originate as the result of the branching of hyphae which grow out from the base of the ascogonium—from the cells below the ascogenous cell, which I have called the stalk of the archicarp (FIG. 9, A). The ascogonium is quickly and completely enclosed by a thick protective layer. This peridium is not broken open at the apex of the young fruit by the upward thrust of the paraphyses but remains entirely closed until the spores are ripe and the asci then push their way up through the enveloping layer. The young hymenium is not exposed to view by the breaking open of an outer wall. The first appearance of the young fruit is that of a smooth globular structure, and later one discovers the tips of asci pushing up between the cells of the upper surface. Sections of entirely closed fruits often show several well formed asci with the eight spores nearly ready for dispersal (FIG. 9, A). The hypothecium is rather poorly developed. The asci often arise from a point below the ascogenous cell since the ascogenous hyphae grow downward as well as upward. My diagram shows to what a large extent the asci occupy the inner space of the fruit. *Ascobolus immersus* and *A. Leveillei* have much the same sort of ascocarp and originate from the same kind of an ascogonium. From the data just given it is plain that further subdivisions of the two main types of apothecia can be distinguished.

According to Overton (70) the fruit body of *Thecotheus* is a compound apothecium. Baur (8, 9), Darbishire (32), and others have described many species of lichens in which several ascogonia take part or are present at least in the formation of each apothecium. *Ascodesmis* and *Pyronema* are the well-known cases where the rosette of sex organs arises as the result of the dichotomous branching of single hyphae. Ramlow (73) concludes that where more than one ascus is found in *Thelebolus* this came about by accidental inclusion of two or three ascogonia in the same fruit, thus simulating what one frequently finds in *Helotium citrinum* and *Pyronema confluens* although in the latter form each of the fusing apothecia is in itself compound.

If we apply these data as to the method of origin of the ascocarp in estimating the value of current classifications of the Ascomycetes we must conclude that the arrangement in a linear series of the

Plectascineae and Perisporiaceae with cleistocarps, the Pyrenomycetes with pyrenocarps, and the Discomycetes with apothecia or discocarps is quite misleading. Considering the vast number of types whose development is yet unknown it would be premature to attempt a final arrangement of the groups along new lines, but in view of the overwhelming evidence in favor of the Floridean origin of the group the possibility that the apothecium as found in the lichens is primitive must certainly be considered. It should be borne in mind, however, that there are Pyrenomycetes like *Polystigma* and pyrenomycetous lichens like *Pyrenula* with primitive types of archicarps and spermatia. The character and rela-

FIG. 12

FIG. 13

FIG. 12. Apothecia of *Ascobolus magnificus*. Photomicrograph of young fruit bodies grown on agar, showing the pore-like opening at the apex and the fluffy white exterior; at this stage no "hooks" or young asci are to be found. Magnified three times.

FIG. 13. Apothecia of *Ascobolus magnificus*, both young and mature fruits, natural size. The brilliant white margin shown in this photograph is very characteristic of this species.

tive development of the trichogyne is perhaps to be regarded as more significant in determining phylogeny than the form of the ascocarp.

The evidence furnished by the trichogyne with all its variations in the Laboulbeniaceae and the other Ascomycetes seems to be sufficient ground for assuming that the Ascomycetes have been derived from the Florideae. Vuillemin (92) would derive them from the ancestors of the Florideae, perhaps from some form

as far back as *Coleochaete*, and from this remote origin would have two parallel lines of development, one leading up to the red algae, the other to the Ascomycetes. This is leaving to the "tendencies to parallelism" the entire explanation of the obvious similarities of the various other structures in both groups. Bucholtz (21), concentrating his attention on the possible evolution of the ascus in such a case as *Endogone*, also explains the trichogyne as due to accidental "parallelism" in development.

We can arrange a series of the forms best known as to their development which shows a progressive shortening of the trichogyne and a corresponding reduction in the number of the antheridia and their gradual shifting towards a position nearer the oögonium: *Collema microphyllum*, *Physma compactum*, *Collema pulposum*, *Ascobolus carbonarius*, *Thecotheus Pelletieri*, *Ascobolus magnificus*, *Lachnea stercorea*, *Pyronema*, *Ascodesmis*, *Sphaerotheca*.

In *Collema microphyllum* the spermatia are developed at some distance from the trichogyne which is active only in reaching the surface of the thallus. The spermatia are borne to the trichogyne through the agencies of water and wind. In *Physma compactum* the trichogynes grow up around the spermogonium. The spermatia are separated from the trichogynes by only a short distance, and the apothecium is developed within or around the old spermogonium. In *Collema pulposum* we find the antheridial branches scattered throughout the thallus, the spermatia remain loosely attached to the stalk and the trichogyne has become the active structure in seeking out the spermatium. The old spermatiophore and trichogyne may or may not become included within the space occupied by the apothecium (FIG. 7). In *Ascobolus carbonarius* the antheridial conidia are distributed at various places through the mycelium bearing the ascogonium and are never set free from the stalk. Instead of clusters of spermatia being borne on one stalk we find only a spore-like "antheridium." The trichogyne grows out to the "antheridium" in much the same way as in *Collema pulposum*. The entire archicarp is finally enclosed in the enveloping hyphae in the early development of the apothecium. Here too we find a much larger number of antheridia than trichogynes developed. A further stage in this reduction and shortening of the trichogyne is found in *Ascobolus magnificus*, where generally

only one antheridium is developed in close proximity to the ascogonial branch. The trichogyne is a much thicker structure of about eight short cells, but it has sufficient length to reach the antheridium to which it applies itself. The trichogyne of *Lachnea stercorea* is somewhat shorter than that of *Ascobolus magnificus*, having about one half as many cells. It apparently fuses with the antheridium without first coiling partly about it. From this stage to *Pyronema* is but a short step where the trichogyne is reduced to one long cell, which we may imagine arose by omitting the cross walls. Reduction has gone on still further in *Ascodesmis*, where the antheridium coils tightly about the ascogonium and the trichogyne is reduced to one short cell. The final step we find in *Sphaerotheca* where the male nucleus travels directly from the antheridium into the oögonium without the aid of any intervening structure.

There are a number of forms in which the ascogonium is prolonged into a trichogyne, although no antheridium is known to exist. In many of the forms in which the trichogyne is most prominent as a multicellular structure at the end of the archicarp we find that several cells of the ascogonium give rise to ascogenous hyphae. In all of the lichens in which this feature has been studied several cells of the ascogonium are connected by large openings and all the cells so connected are ascogenous cells (FIG. 7). Three or four of the first cells beyond the stalk of the ascogonium of *Ascobolus carbonarius* are ascogenous. Cutting (27) states that several cells of the ascogonium in *Ascophanus carneus* give rise to fertile hyphae. Overton (70) has reported the same for *Thecotheus*, and Miss Fraser (44) for *Lachnea cretea*. I have no doubt that the same is true in *L. abundans* and *L. melaloma* although I have not as yet determined this point fully. The list of forms with more than one ascogenous cell is as follows: the lichens, *Ascobolus carbonarius*, *A. pusillus*, *A. glaber*, *Saccobolus*, *Ascophanus carneus*, *Thecotheus Pelletieri*, *Lachnea cretea*, *L. abundans*, *L. melaloma*, *Aspergillus*, *Gymnoascus*, *Ascodesmis* (?).

In *Ascobolus furfuraceus*, *Lachnea scutellata*, *Lasiobolus equinus*, and *Pyronema*, only one cell of the ascogonium bears ascogenous hyphae. In *Lasiobolus pulcherrimus* there is but one ascogenous cell, though the ascogonium is prolonged into a structure of seven

or eight cells. Arranging these forms with only one ascogenous cell in the order of the complexity of the archicarp we find the following series: *Lasiobolus pulcherrimus*, *Ascobolus furfuraceus*, *A. immersus*, *Lachnea scutellata*, *Lasiobolus equinus*, *Ascobolus Winteri*, *A. Leveillei*, *Pyronema*, *Thelebolus*, *Sphaerotheca*.

If we compare the second and third groups above, especially *Ascobolus carbonarius* with *A. furfuraceus* we may get some light on the nature of the entire ascogonium in the latter species, that is, on the question whether the part beyond the ascogenous cell is to be considered morphologically as a trichogyne.

It is certainly very difficult to attempt to homologize the crosier and nuclear fusions in the young ascus with the oöblastema and auxiliary cells and fusions of the *Dudresnaya* type, but it is clear that both involve the same physiological or nutritive conditions. After the fusion of the oöblastema filaments with the auxiliary cells which are gorged with nourishment we find the conditions required for the production of well nourished filaments producing spores. The vegetative nuclear fusions in the ascogenous hyphae provide a large amount of nuclear substance to maintain the "nucleo-cytoplasmic equilibrium" of a large spore mother-cell. In other words the secondary fertilizations of the red algae provide conditions suitable to the formation of groups of carpospores just as the hook phenomena and nuclear fusions in the Ascomycetes lead to the production of ascospores.

We must consider the outgrowths of the carpogonium in all forms of the red algae as homologous structures. The question as to whether or not reduction occurs at the germination of the fertilized egg in *Nemalion* is not necessarily a vital one in this connection. The oöblastema filaments of the *Dudresnaya* group are then homologous with the sporogenous hyphae of *Dermonema*, *Nemalion*, etc., although they do not give rise, for example in *Gloiosiphonia*, directly to carpospores. In the Ascomycetes, *Dudresnaya*, and *Gloiosiphonia* both ascospores and carpospores are produced only after secondary fusions have occurred, and the suggestion is strong that the ascogenous hyphae are homologous with the oöblastema filaments. The very short oöblastema outgrowths in *Harveyella*, *Erythrophyllum*, *Prionitis*, correspond to the long much branched oöblastema of *Dudresnaya*, and among the

Ascomycetes we have the greatest variation in the relative development of the ascogenous hyphae.

It is of course of vital importance to determine where the spermatium nucleus unites with the egg, in view of the fusions between the cells of ascogonia followed by many nuclear divisions such as Miss Bachmann observed. Each of the several fused cells gives rise to ascogenous hyphae (FIG. 9). One sexual act has served to fertilize several cells, exactly as in *Dudresnaya* the fertilization of a single egg ultimately leads to the production of several masses of carpospores.

The hypothetical cases described by Schmitz to provide for possible variations in the reproductive processes which might later be discovered are suggestive. He imagined that the "second sexual act" might by degeneration disappear entirely, leaving conditions just what they are in the primitive forms like *Nemalion*. In case of a failure in the first sexual act due to non-development of spermatia Schmitz conceived that the spermatium mother-cell might grow out into a branched or unbranched male hypha which could perhaps fertilize the auxiliary cell (cf. Sachs' figure of *Ascobolus furfuraceus*). In such cases the carpogonium in time would probably not develop a trichogyne and might even tend to disappear. In case the spermatium mother-cell were not formed the carpogonium itself might grow out directly into male hyphae which could bring about the same end result, the fusion with the auxiliary cell, which might be either an end cell (*Dudresnaya purpurifera*) or an intercalary cell (*D. coccinea*). Schmitz saw a similarity between the Collemaceae and the Cryptonemiaceae but believed that reduction had in some cases already occurred to the extent that the spermatia were no longer developed. In other cases the first sexual act has been entirely suppressed, the second only functioning. This case would correspond to that of the Exoascaceae as we know them. Having in mind the scolecite or ascogone of *Ascobolus* and *Lasiobolus* with the curiously branched hypha, the pollinodium, coiling about its upper end as described by Woronin, Borzi, and Janczewski, Schmitz conceived the ascogenous cell, "the mother-cell of the ascogenous hyphae," to be homologous with the auxiliary cell in the Cryptonemiaceae which is fertilized by the "second sexual act." Reduction in other

cases has gone on so far that the second sexual process has also disappeared so that the auxiliary cell, ascogenous cell itself, whether it can be distinguished from ordinary hyphae by its special form or not, may give rise directly to the spore fruit (*Thelebolus*, *Teichospora*). These speculations of Schmitz regarding the sexuality of the Ascomycetes do not apply to the facts as since worked out and are treated much as Heydrich's theory (54) of the origin of the tetraspore mother-cell is today. Not knowing of the nuclear fusion in the ascus it did not occur to Schmitz that the ascogenous hyphae of *Ascobolus* were to be compared to the oöblastema filaments. He considered them merely as equivalent to the gonimoblasts growing out of the fertilized auxiliary cells to produce carpospores. To him each cystocarp of *Dudresnaya* would be represented by an apothecium, the one or two rows of carpospores in *Cruoriopsis* would be much reduced cystocarps. The apothecium should, however, correspond to a whole nemathecium of *Dudresnaya* cystocarps packed together in one compound fruit. The fruit of *Cruoriopsis* would in reality be a very good counterpart of the apothecium of *Ascobolus magnificus*, *Pyronema*, or *Collema*. One sexual process, or several independent and equal in *Pyronema*, followed by a large number of secondary fusions (auxiliary cells with oöblastema, nuclear or cell fusions at the end of the ascogenous hyphae) gives rise to what we know as the spore fruits of the Ascomycetes.

The attempt to connect the Ascomycetes with the red algae on the basis of superficial resemblances between the ascocarp and cystocarp is entirely misleading. Schmitz pointed out that this system as proposed by Agardh (1), in which the characters of the thallus and cystocarp were made the basis of classification, was entirely inadequate for the purpose of showing phylogenetic relationships. The system proposed by Schmitz, slightly modified by Oltmanns and recently analyzed by Daines, makes no use whatever of the characters of the mature cystocarp in circumscribing the five large groups into which the Florideae are subdivided. This new system is based almost entirely on the morphology of the outgrowths of the fertilized egg together with the origin and disposition of the auxiliary cells and the development of the fusion and central cells. A practical example of the application of these

principles is furnished by Sturch (87) who transfers the genus *Harveyella* from the Nemalionales to the Gigartinales on the basis of the method of development of the procarp and the formation of the auxiliary cell, *i. e.* processes that are concerned with fertilization and the development of the sporophyte. Twiss (91) would transfer *Erythrophyllum* to the *Gigartinaceae* and Daines (28) *Prionitis* to the Ceramiales for like reasons. De Bary and Janczewski maintained on the same ground that the nature of the ascogonium and the method and degree of its development rather than the form of the mature ascocarp furnish the best basis for the determination of homologies in the Ascomycetes.

New data as to the morphology of the ascogonium and trichogyne are accumulating rapidly. Investigation of a great number of species ranging from the gelatinous Collemaceae to the dry Cladoniaceae, or the hard and black Graphidiaceae, including both discomycetous and pyrenomycetous forms, discloses the fact that a vast majority of these fungi are provided with trichogynes, and where no such structure has been found, an ascogonium has generally been more or less clearly recognized. It is not improbable that further research will disclose many other interesting transition forms such as we now find in *Collema pulposum*, *Ascobolus carbonarius*, and *Ascobolus magnificus*.

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Professor of Botany.

COLUMBIA UNIVERSITY,
NEW YORK CITY.